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Why is the early bird early? An evaluation of hypotheses for avian dawn-biased vocal activity

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Bird species vary widely in their diurnal vocalization patterns, and the drivers of this variation are not well understood. Using passive acoustic monitoring, we examined species-specific vocal activity patterns at dawn and dusk for a tropical bird community in the Western Ghats biodiversity hotspot in India. We tested whether environmental factors (e.g. signal transmission conditions, ambient light, and resource availability) and social factors (e.g. territoriality) best-explained patterns of diurnal variation in vocal activity. Overall, we found that species-specific vocal activity was significantly higher at dawn (p < 0.05). Phylogenetic generalized least squares regressions revealed that territoriality and diet both predicted stronger dawn-biased activity. Specifically, highly territorial birds (standardized effect size (SES) = 1.20, lower donfidence interval (LCI)= 0.24, upper confidence interval (UCI) = 2.16, p = 0.01) and omnivores (SES = 0.82, LCI = −0.04, UCI = 1.68, p = 0.06) had higher levels of vocal activity at dawn. Surprisingly, we failed to find any evidence in support of environmental factors in explaining dawn-biased vocal activity. Our multi-taxon approach allowed us to assess the vocal activity patterns for an entire tropical bird community. Future research must incorporate additional geographic locations and combine visual and aural observations to better understand the drivers of diurnal variation in vocal activity.

This article is part of the theme issue 'Acoustic monitoring for tropical ecology and conservation'.

1. Introduction

Vocalizations are a crucial aspect of bird behaviour and serve various communication purposes, including mate attraction, territorial signalling, competition and prey–predator warning systems, to name a few [1–3]. Bird species vocalizations vary spatially and temporally. Across geographic space, bird populations can possess distinct vocal dialects [4]. Birds also vary their vocalization patterns depending on the month of the year—e.g. breeding months for passerines are associated with higher rates of singing [5]. Even within the same site, bird species can vary their vocal output as a function of time of day. Voigt *et al*. [6] found that male White-browed Sparrow-weavers (*Plocepasser mahali*) had higher rates of vocalizations earlier in the day than later. Male Savannah sparrows (*Passerculus sandwichensis*) showed higher song output during the dawn chorus in the pre-breeding period [7]. Today, a whole body of literature has largely focused on the mechanisms behind the dawn chorus—a period of high vocal activity early in the morning [8–11], while limited research has examined diurnal variation in bird species vocalizations and the factors responsible for these differences.

A combination of environmental, social and physiological factors have been proposed to explain differences in vocalization patterns at different

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times of day (i.e. dawn and dusk). From an environmental perspective, several highly interrelated factors, such as air quality and signal transmission conditions, levels of ambient light and resource availability, have been proposed as crucial determinants of variation in diurnal vocalizations [12–17]. For example, the acoustic transmission hypothesis [12,13] suggests that wind velocity, temperature gradients and associated signal transmission conditions are more favourable earlier in the day for maximum signal propagation. On a related note, the inefficient foraging hypothesis [14,15] suggests that limited light levels closer to dawn would result in inefficient foraging; hence, it would be advantageous for species to utilize this time for vocalizing rather than foraging, although previous tests of this hypothesis have not considered dynamics at dusk. In addition, resource and prey availability may indirectly or directly impact vocal activity owing to intra- and inter-species vocal signalling to communicate the presence of resources or to defend them from others [16–18]. On the other hand, diurnal variation in species vocalization may also be explained by the social functions they confer. Staicer *et al*. [11] proposed that singing earlier in the day could act as an intersexual function for attracting or guarding mates, advertising and defending territories [7,19,20] and adjusting social relationships (e.g. group-living birds) [6,21,22]. While environmental and social factors are the focus of this study, we add that such factors may be expressed through other mechanisms, like hormonal regulation of testosterone and other physiological changes [11,23,24].

Birds are a diverse taxonomic group and highly accomplished vocalizers, making them ideal candidates for examining the patterns of diurnal variation in vocal activity. Historically, it has been difficult to quantify the temporal patterning of vocalizations because it would require large numbers of skilled human observers in the field over extended periods of time. In addition, vocal activity often occurs at a rate that makes it difficult for a human to track and record it in real time. Passive acoustic monitoring has made it possible to collect vocalization data across space and time and to analyse those data in a detailed, controlled and replicated manner [25–27]. Using multiple autonomous recording units collecting data across numerous locations simultaneously, we can now obtain large amounts of species-specific acoustic data for an entire community. We used passive acoustic monitoring to examine species-specific vocal activity patterns across dawn and dusk for a tropical bird community in the Western Ghats biodiversity hotspot. The Western Ghats is home to hundreds of bird species, several of which are rare, endangered and endemic to this region [28]. By analysing acoustic data for 69 species of birds across 43 locations from a mid-elevation wet evergreen rainforest in the Western Ghats, we asked: [1] how does species vocal activity vary between dawn and dusk? And [2] is the difference in vocal activity between dawn and dusk best explained by environmental factors (signal transmission conditions, light levels and resource availability) and/or by social factors (extent of territoriality)? (Refer to table 1 for a list of hypotheses and expectations.)

2. Material and methods

(a) Study area and acoustic data collection

To compare vocal activity between dawn and dusk, we obtained acoustic data from 43 unique rainforest sites in the Valparai plateau of the Western Ghats biodiversity hotspot (electronic supplementary material, figure S1 and electronic supplementary material, table S1). The Valparai plateau is situated in the Anamalai hill range within the Western Ghats and primarily consists of mid-elevation tropical wet evergreen rainforests (*Cullenia exarillata–Mesua ferrea–Palaquium ellipticum* type; elevational breadth: 700–1400 m above sea level [29]). The plateau is a typical example of a human-modified biodiverse landscape in India and is home to hundreds of species of rare and endemic flora and fauna and supports the livelihoods of thousands of people [30]. Acoustic data were collected as part of a previous study (see [31]). At each of the 43 sites chosen following a study design that accounted for topography, flora, physiognomy and other factors, we deployed a single AudioMoth audio recorder [32] to collect acoustic data. Recorders were programmed with a sampling rate of 48 kHz and a gain of 40 dB to record data for seven consecutive days at each location (recording cycle: 4 min ON and 1 min OFF). The audio data were collected between March 2020 and January 2021. Within this temporal period at each location, the recorders collected data over four cycles, with a gap of two weeks between the cycles. Each cycle corresponded to seven consecutive days of data collection. Owing to the southwest monsoons, no acoustic data were collected between June 2020 and October 2020. Each recorder was deployed such that no two recorders were less than 160 m apart. This distance was determined as the closest distance that reduced levels of spatial autocorrelation [31].

(b) Acoustic data processing

A subset of the acoustic data was reviewed to identify every vocalizing bird species in the recording and how often they were detected. We obtained the subset of acoustic data by randomly selecting three non-consecutive days between March 2020 and May 2020 and three non-consecutive days between November 2020 and January 2021. For each day, we extracted two continuous 16 min recordings—once between 06:00 and 08:30 and once between 16:30 and 18:30 , which represent periods of high vocal activity after sunrise and before sunset, respectively. Sampling windows were chosen to capture a similar amount of time right after dawn and right before dusk to ensure that they were comparable. The reason for choosing 16 min as the duration of the acoustic subset data was for comparison with human point-count surveys at the same location for another ongoing study. These 16 min were further broken down into 10 s audio segments to ease bird species identification and further audio processing. Using Raven Pro [33], we visually and aurally reviewed each 10 s audio segment to identify the presence and absence of every bird species. Two expert reviewers who were knowledgeable about bird vocalizations in this region annotated the acoustic data. Any ambiguous vocalizations were confirmed with an additional expert (Dr T R Shankar Raman at the Nature

Table 1. A list of environmental and social hypotheses to explain diurnal variation in vocal activity along with predicted and observed results.

factor	hypothesis	mechanism	prediction	observed results
environmental	acoustic transmission hypothesis [12,13]	air quality and signal transmission conditions are more favourable for singing/calling earlier in the day than later	species that vocalize at higher frequencies will have higher rates of vocal activity at dawn for maximum signal transmission and least attenuation; this hypothesis predicts a positive relationship between dawn vocal activity and the peak frequency of a species	we observed no significant relationship between the peak frequency of vocalizations and dawn-biased vocal activity
	inefficient foraging hypothesis [14]	species utilize periods of low ambient light at dawn and dusk to sing/call, focusing foraging during times of day when the sun is up and light levels are high	vocal activity will be similarly high after sunrise and before sunset, as both times have low light and poor foraging efficiency	dawn vocal activity is substantially higher than dusk vocal activity; since birds are not signalling as actively in low-light evening conditions, the visual efficacy of foraging alone does not fully explain the timing of bird song
	foraging guild [17]	singing rates will vary as a function of prey availability and prey activity	invertivores are predicted to have higher rates of vocal activity at dawn when insects are less active	omnivorous species marginally explained higher levels of dawn vocal activity; however, the importance of this association across communities and ecological mechanism of this association remains to be elucidated
social	territorial defence hypothesis [11]	dawn song is a form of 'extra vigorous keep-out signal' that serves to defend and advertise their territories to prospecting males after a period of inactivity at night	highly territorial species have higher vocal activity at dawn than at dusk	highly territorial bird species significantly explained higher rates of vocal activity at dawn.
	social dynamics hypothesis [11]	dawn chorus serves as an interactive communications network that helps to adjust social relationships between neighbours	communal signallers will have higher vocal activity at dawn than at dusk	

Conservation Foundation). Detections were defined as the presence of the call/song of a bird within a 10 s recording. Even if a bird sang/called for longer than 10 s, we marked the species as present in each of the consecutive 10 s recordings across the 16 min of randomly subset data. In this fashion, 138 h of acoustic data were manually annotated and processed to identify every bird species across the dawn and dusk recordings. This processing resulted in the identification of 120 unique bird species.

(c) Vocal activity

Vocal activity is a measure of calling/singing for a specific time period and was calculated for each species at dawn and dusk separately. This species-specific metric was calculated as the total number of acoustic detections of that species across all 'visits' to all sites divided by the total number of acoustic recordings processed. Dividing the total number of acoustic detections by the number of acoustic recordings processed allows us to control for sampling effort. This process was repeated separately for each species across the dawn recordings and the dusk recordings, respectively. We removed species detected across fewer than 20 unique acoustic recordings from our analysis. This process ensured that we only included species that were well-sampled, resulting in 69 species for further analysis. We then used a Wilcoxon test to compare whether vocal activity significantly differed across species between dawn and dusk.

(d) Acoustic frequency of vocalization

To test the predictions of the acoustic transmission hypothesis, we obtained data on the peak frequency at which a species vocalizes [12,13]. Microclimatic conditions (such as air turbulence, wind, humidity and temperature) can cause significant signal attenuation and degradation, especially of high frequencies [12]. Therefore, we predicted that species vocalizing at higher frequencies would be more vocal at dawn than at dusk since signal transmission conditions are hypothesized to be better earlier in the day than later (table 1). To obtain data on the peak frequency of calls/songs, we extracted high-quality vocalizations by manually combing through the acoustic data (both the subset of annotated data and other audio data that had not been annotated). We define high-quality vocalizations as signals with minimal background noise and signal interference. Here, we defined a signal as a unique call or a song of a species when there was less than 1 s interval between their notes. We considered each song or call to be made up of a collection of notes. Each of these high-quality vocalizations was demarcated using selection boxes in Raven Pro [33]. Through this process, we extracted approximately 20 000 high-quality vocalizations across 114 species. For further analysis, we ensured that each species selected in our study ($n = 69$, see previous section) had at least five high-quality vocalizations. Using the peak frequency measurement in Raven Pro, we extracted the highest-amplitude frequency of a selected vocalization. Following this process, we obtained a median value of the peak frequencies for each of the 69 species for further analysis (electronic supplementary material, table S2).

(e) Ambient light at the time of vocalization

To test the predictions of the inefficient foraging hypothesis [14], we examined the association between the timing of vocalization and a species' vocal activity. Since we did not obtain data on actual light levels at each site, we assumed that the timing of vocalization is a proxy measure for the ambient light level. We extracted the timing of vocalization as follows: for each unique site and date for which acoustic data were manually annotated, we used the *suncalc* package [34] within the R Programming Environment [35] to obtain nautical dawn and nautical dusk times for each unique site–date combination. To define this proxy measure of ambient light level, we calculated the ‘time to darkness’ for each recording. For example, both a recording that began 45 min after nautical dawn and a recording that ended 45 min before nautical dusk would have a time to darkness of 45 min. However, we acknowledge that this assumption does not necessarily reflect actual light levels at all times. While the timing of vocalization cannot completely capture on-site light levels, we believe that timing is the closest proxy to ambient light in lieu of on-site light measurements.

(f) Foraging guild

To extract data on foraging guild or diet type, we used the AVONET trait database [36] for each of the 69 species in our study. Species categorized as frugivore ($n = 10$), omnivore ($n = 17$) or invertivore ($n = 35$) were retained in our study (amounting to 62 out of a total of 69 species for the phylogenetic generalized least squares (PGLS) regressions), and those species categorized as aquatic predators, granivores, nectarivores or vertivores were removed owing to a small sample size.

(g) Extent of territoriality and levels of communal signalling

To test the social factors that may best explain diurnal variation in vocal activity between dawn and dusk, we extracted data on the extent of territoriality and communal signalling for each species from Tobias *et al.* [37]. According to this dataset, territoriality was scored as ‘none’ (species that do not defend territories, or defend very small areas around nest sites, song or display posts only), ‘weak’ (species that are vocal and aggressive only for some part of the year, have broadly overlapping home ranges or sometimes join mixed flocks without defined spatial ranges) and ‘strong’ (species that defend and maintain territories throughout the year). Species were also classified as ‘communal signallers’ (which includes species that produce acoustic signals in groups—either as duets (two individuals) or choruses (three or more individuals) by both males and females) and as ‘non-communal signallers’ (which includes species that sing as single individuals and not communally).

(h) Phylogenetic generalized least squares regressions

To determine which factor (environmental or social) or combination of factors best predicted the diurnal variation in vocal activity, we ran PGLS regressions using the *nlme* package [38]. We chose PGLS because it helped us control for non-independent observations owing to phylogenetic relatedness [39]. Using https://birdtree.org [40], we downloaded 100 phylogenetic trees (Hackett backbone) of the 69 species in our dataset. We then computed the maximum clade credibility tree from this sample using the *phangorn* package [41]. We fitted a phylogenetically informed model with a Brownian correlation structure (lambda set to 1) [42]. We ran a multivariate model with all the predictor variables. Our correlation test revealed a significant correlation between territoriality and sociality ($r = 0.66$), which led us to remove sociality from the multivariate model. For the multivariate model, we considered foraging guild type and territoriality as categorical fixed effects and median peak frequency (scaled value) and ambient light (scaled value of median time to darkness) as continuous fixed effects. The full multivariate model was the best-fitting model compared with univariate models (based on Akaike information criterion (AIC) values; electronic supplementary material, table S3) and henceforth, we refer to and report the full multivariate model results with all predictors.

All analyses are publicly available and can be reproduced using code and data from this link: https://github.com/vjjan91/diurnal-Acoustics. Unless otherwise specified, all statistical analyses were performed using the R Programming Environment [35].

3. Results

In the community of Western Ghats birds that we studied, the amount of vocal activity was significantly higher at dawn compared with dusk (Wilcoxon test; $p < 0.05$; figure 1a). Acoustic signals of four species were detected only at dawn—the

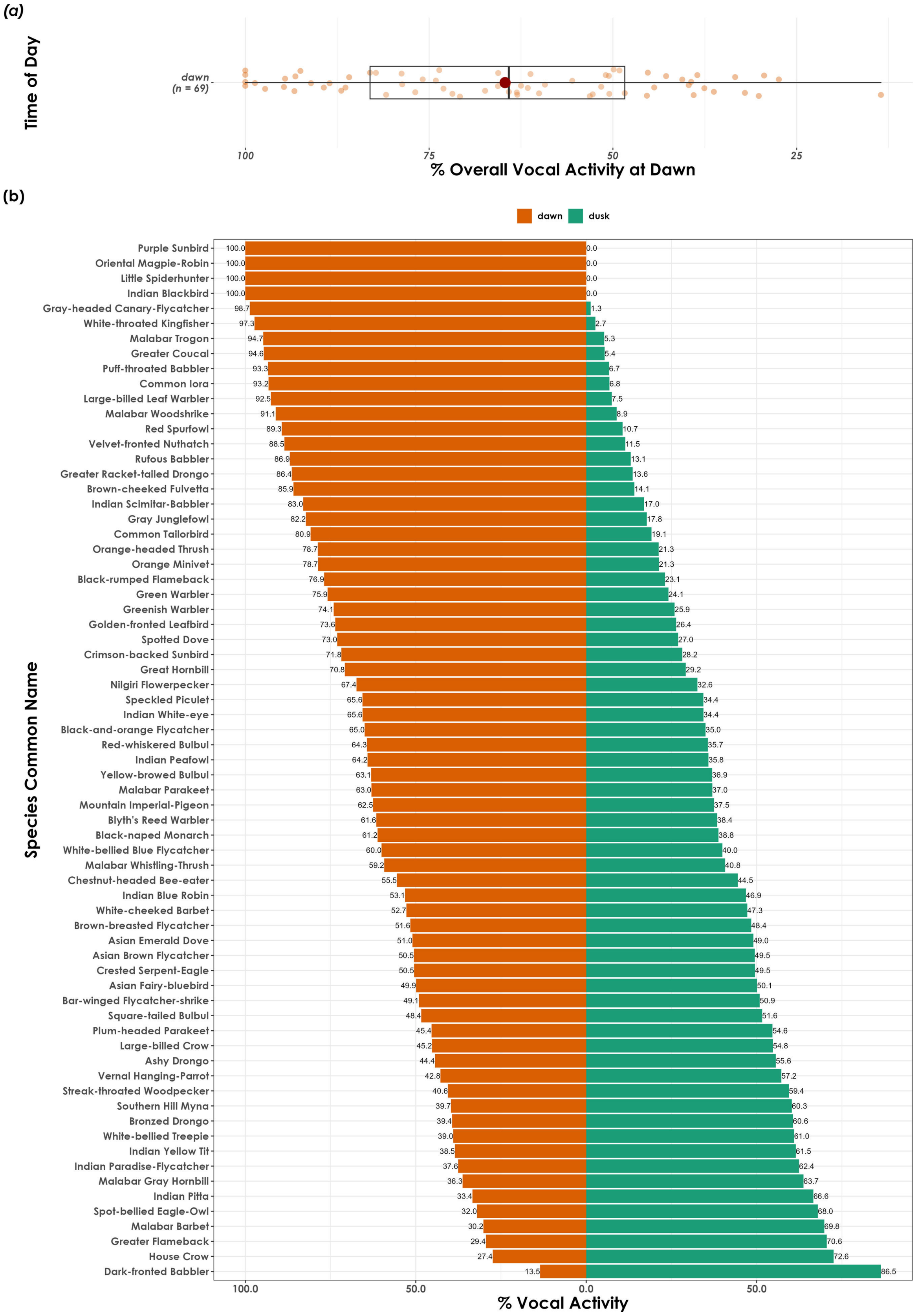

Figure 1. (a) Vocal activity was significantly higher at dawn than dusk across a tropical bird community in the Western Ghats. (b) Species-specific vocal activity patterns (note: species here that have 100% dawn-associated vocalizations represent only what was captured in our annotation of acoustic data and our results do not suggest that these species do not vocalize at dusk).

Indian blackbird (*Turdus simillimus*), the little spiderhunter (*Arachnothera longirostra*), oriental magpie-robin (*Copsychus saularis*) and the purple sunbird (*Cinnyris asiaticus*). Twenty species had vocal activity that was substantially higher at dawn (>80% of vocal activity at dawn compared with dusk). Notable representatives include the gray-headed canary-flycatcher (*Culicicapa ceylonensis*), greater coucal (*Centropus sinensis*), large-billed Leaf Warbler (*Phylloscopus magnirostris*) and puff-throated babbler (*Pellorneum ruficeps*; for a complete list of species, see figure 1b). The dark-fronted babbler (*Rhopocichla atriceps*) was the only species with significantly higher vocal activity at dusk (>80% of vocal activity at dusk compared with dawn; figure 1b).

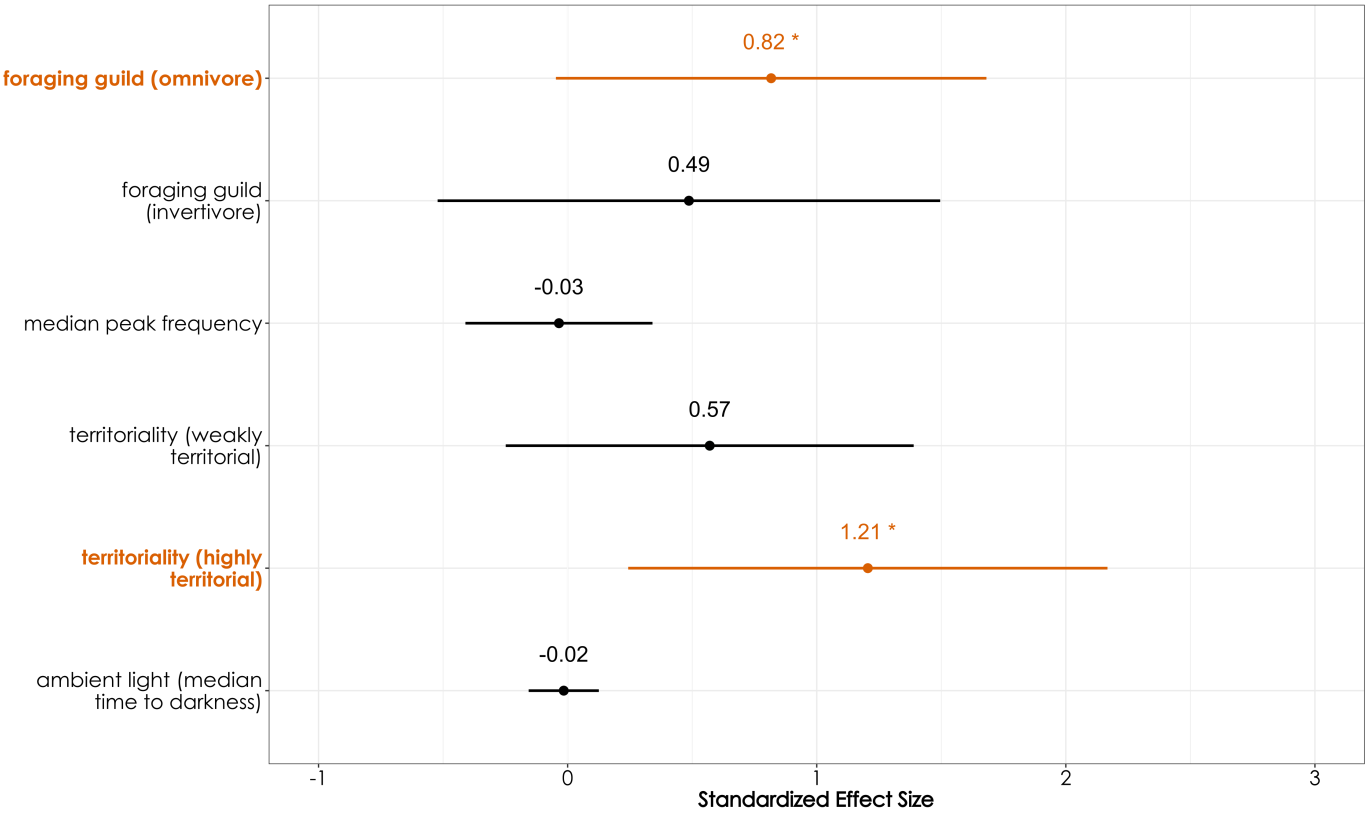

Figure 2. Predictors of dawn-biased vocal activity. Asterisks denote significant ($p < 0.05$) associations. Dots represent standardized model estimates and error bars denote 95% confidence intervals for the PGLS regressions. An orange dot represents a significant association. Highly territorial birds (reference category: non-territorial birds) and omnivorous bird species (reference category: frugivorous birds) had significantly higher dawn-biased vocal activity.

Our multivariate PGLS regressions revealed the combination of environmental and social factors that best explained dawn-biased vocal activity across species. Compared with frugivores, omnivores had a marginally significant higher vocal activity at dawn (SES = 0.82, LCI = −0.04, UCI = 1.68, $p = 0.06$; figure 2 and table 2). Compared with non-territorial bird species, highly territorial birds had a significantly higher dawn-biased vocal activity (SES = 1.20, LCI = 0.24, UCI = 2.16, $p = 0.01$; figure 2 and table 2). Ambient light (median time to darkness) and median peak frequency were not significantly associated with vocal activity at dawn.

4. Discussion

In this study, we investigated whether extrinsic (environmental and social) factors drive patterns of diurnal variation in vocal activity for a tropical rainforest bird community. The percentage of vocal activity was significantly higher at dawn across the vast majority of species examined. Highly territorial and omnivorous species were most strongly dawn-biased in their vocal activity.

Highly territorial bird species, for example, brown-cheeked fulvetta (*Alcippe poiocephala),* Indian scimitar babbler (*Pomatorhinus horsfieldii*) or white-bellied treepie (*Dendrocitta leucogastra*) had higher dawn-biased vocal activity compared with non-territorial birds. Previous studies in winter wrens [19], common nightingales [20,43] and savannah sparrows [7] show that species rely on vocal communication at dawn to defend and maintain territories and thus lend support to the above result. In our study, several species that were highly territorial were also species that signalled communally ($n = 10/15$). Since territoriality and communal signalling are highly correlated, we did not incorporate communal signalling as an explanatory variable in our PGLS analysis [21,22,44].

Diet was a marginally significant predictor of dawn-biased vocal activity. Omnivorous birds (e.g. red-whiskered Bulbul (*Pycnonotus jocosus*) and yellow-browed bulbul (*Iole indica*)) showed a significantly higher dawn-biased vocal activity compared with frugivorous birds. Previous research in the Western Ghats shows that several omnivorous and invertivorous birds participate in mixed-species foraging groups, where different species forage together by relying on vocal cues for predator avoidance and vigilance [45,46]. Such mixed-species foraging groups are especially active close to dawn compared with later in the day or close to dusk in this landscape [47], which may in turn be driven by resource availability.

(a) Environmental factors do not explain dawn-biased vocal activity

For a few decades now, scientists have hypothesized that environmental conditions, specifically microclimatic conditions later in the day, can attenuate and degrade animal signals, thereby hindering sound propagation and communication [12,13]. However, our results suggest that birds with high-frequency attenuation-prone signals are not more likely to signal at dawn

Table 2. The results of phylogenetic least squares regression using a multivariate model with all predictor variable.

predictor variable		estimates	standard error	upper confidence level	lower confidence level	*p*-value
ambient light	median time to darkness	−0.016	0.070	0.125	−0.156	0.824
territoriality (reference category = non-territorial)	highly territorial	1.205	0.478	2.167	0.243	**0.015****
	weakly erritorial	0.570	0.407	1.389	−0.248	0.168
peak requency	median peak frequency	−0.035	0.187	0.341	−0.410	0.853
foraging guild (reference category = frugivores)	invertivore	0.487	0.502	1.496	−0.522	0.337
	omnivore	0.818	0.430	1.681	−0.047	**0.063***

Bold highlighting indicates significant values.
*, *p*-value less than or close to 0.05; **, *p*-value less than 0.01.

compared with species that vocalize at other frequencies since we found no statistically significant association between vocal activity and median peak frequency (electronic supplementary material, figure S2). We also found that ambient light (timing of vocalization) did not significantly explain the diurnal variation in vocal activity across species, contrary to the predictions of the inefficient foraging hypothesis [14]. If the inefficient foraging hypothesis explained the timing of behaviour, we expected reciprocal peaks of activity both at dawn and at dusk when similar light conditions would impose similar constraints on visual foragers. Studies focused on the factors that determine the onset of the dawn chorus have also suggested that eye size and vegetation structure are key predictors [15,48]. We have yet to consider vegetation structure, but we recognize the potential role of structure and composition in explaining vocal activity variation (e.g. the acoustic adaptation hypothesis [49,50]). Our study did not curate data on light levels and we used a proxy measure for time to darkness, and we suspect that a combination of other factors, including resource availability, foraging guild and time of year (breeding or non-breeding times), may better predict vocal activity rates.

(b) Limitations and conclusions

While passive acoustic monitoring allowed us to examine the vocal activity of an entire bird community simultaneously, we lacked on-the-ground behavioural, sexual and social information for species and individuals, which may have provided us with a more robust understanding of vocalizations. While the acoustic data provide evidence for territoriality and diet in explaining dawn-biased vocalizations, a true test of the social as well as environmental hypotheses requires visual observations of foraging, territorial defence and vocalization context. Future research should consider using hand-held recorders and acoustic localization arrays [51] to record the behaviour of multiple individuals during interactions [21,22,52], which can provide insights into social communication and behavioural dynamics. This study focused on predictors of vocalization timing for rainforest birds in the Western Ghats. Even within this study, several of the bird species that were highly dawn-biased are most typically associated with open habitats (e.g. oriental magpie-robin and purple sunbird) rather than with rainforest, suggesting that in other habitats and geographic locations, dusk vocalizations may be observed for such species and other predictors may be more prominent. Species with low vocal activity (especially raptors and nocturnal bird species) were not well-represented in the acoustic analysis, meaning that we are unable to comment on whether similar internal and external factors affect the vocalizations that these species produce.

In an era of rapid human-induced environmental changes, extrinsic factors that were not considered in this study—such as changes in temperature and loss of habitat—may impact behavioural changes, including vocalizations [53]. While we are unaware of how bird species vocalizations in this region may be impacted by varying climatic changes, we are finding that birds vocalize at different frequencies in undisturbed contiguous forests when compared with nearby forest fragments, highlighting the potential effect of habitat fragmentation on vocalizations (Swathi, Hariharan and Ramesh, in preparation). In the future, an integrated study design with microclimate data loggers, hand-held acoustic recorders and passive acoustic monitors can help to assess how environmental changes impact bird vocalizations and associated social interactions, and thereby inform species monitoring efforts.

Several studies have examined hourly variation in acoustic detections throughout the day using visual and aural observations [54]. We are currently working towards incorporating automated identification approaches to obtain hourly data on acoustic detections in the future (e.g. https://www.kaggle.com/competitions/birdclef-2024/). By obtaining such data, we can robustly test environmental and social hypotheses that drive diurnal variation in vocal activity. Such automated approaches also open opportunities to explore seasonal variation as vocal activity patterns may be attributed to different roles in different stages of the breeding season (e.g. [6,7]). To that end, we demonstrate a reproducible approach that relies on passive acoustic monitoring to examine the extrinsic factors influencing diurnal variation in vocal activity.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data and analysis associated with the manuscript can be accessed at [55].

Supplementary material is available online [56].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. V.R.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, validation, visualization, writing—original draft, writing—review and editing; P.S.: conceptualization, formal analysis, investigation, methodology, software, visualization, writing—original draft, writing—review and editing; M.S.: data curation, investigation, methodology, writing—review and editing; L.S.: conceptualization, investigation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests. We declare we have no competing interests.

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References

1. Catchpole CK, Slater PJB. 2008 *Bird song: biological themes and variations*, 2nd edn. New York, NY: Cambridge University Press.
2. Marler P. 2004 Bird calls: their potential for behavioral neurobiology. *Ann. NY. Acad. Sci*. **1016**, 31–44. (doi:10.1196/annals.1298.034)
3. Rogers L, Kaplan G. 2002 *Songs, roars, and rituals: communication in birds, mammals, and other animals*. Cambridge, MA: Harvard University Press.
4. Marler P, Tamura M. 1962 Song 'dialects' in three populations of white-crowned sparrows. *Condor* **64**, 368–377. (doi:10.2307/1365545)
5. Slagsvold T. 1977 Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. *Ornis Scand* **8**, 197–222. (doi:10.2307/3676105)
6. Voigt C, Leitner S, Gahr M, Ter Maat A. 2021 Seasonal and diurnal variation of vocal behaviour in duetting white-browed sparrow weavers. *J. Ornithol*. **162**, 1163–1172. (doi:10.1007/s10336-021-01905-w)
7. Moran IG, Lukianchuk KC, Doucet Stéphanie M, Newman AEM, Williams H, Norris DR, Mennill DJ. 2019 Diel and seasonal patterns of variation in the singing behaviour of savannah sparrows (*Passerculus sandwichensis*). *Avian Res* **10**, 26. (doi:10.1186/s40657-019-0165-6)
8. Wright HW. 1912 Morning awakening and even-song. *Auk* **29**, 307–327. (doi:10.2307/4071038)
9. Allard HA. 1930 The first morning song of some birds of Washington, D. C.; its relation to light. *Am. Nat*. **64**, 436–469. (doi:10.1086/280329)
10. Gil D, Llusia D. 2020 The bird dawn chorus revisited. In *Coding strategies in vertebrate acoustic communication,* Animal Signals and Communication (eds T Aubin, N Mathevon), pp. 45–90, vol. **7**. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-030-39200-0_3)
11. Staicer CA, Spector DA, Horn AG. 2020 24. The dawn chorus and other diel patterns in acoustic signaling. In *Ecology and evolution of acoustic communication in birds* (eds DE Kroodsma, EH Miller), pp. 426–453. Ithaca, NY: Cornell University Press. (doi:10.7591/9781501736957-033)
12. Henwood K, Fabrick A. 1979 A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *Am. Nat*. **114**, 260–274. (doi:10.1086/283473)
13. Wiley RH, Richards DG. 1978 Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol*. **3**, 69–94. (doi:10.1007/bf00300047)
14. Kacelnik A. 1979 The foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. *Anim. Behav*. **27**, 237–241. (doi:10.1016/0003-3472(79)90143-x)
15. Berg KS, Brumfield RT, Apanius V. 2006 Phylogenetic and ecological determinants of the neotropical dawn chorus. *Proc. R. Soc. B* **273**, 999–1005. (doi:10.1098/rspb.2005.3410)
16. Barnett CA, Briskie JV. 2007 Energetic state and the performance of dawn chorus in silvereyes (*Zosterops lateralis*). *Behav. Ecol. Sociobiol.* **61**, 579–587. (doi:10.1007/s00265-006-0286-x)
17. Kacelnik A, Krebs JR. 1983 The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* **83**, 287–308. (doi:10.1163/156853983x00200)
18. Hillemann F, Cole EF, Keen SC, Sheldon BC, Farine DR. 2019 Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds. *Proc. R. Soc. B* **286**, 20182740. (doi:10.1098/rspb.2018.2740)
19. Amrhein V, Erne N. 2006 Dawn singing reflects past territorial challenges in the winter wren. *Anim. Behav*. **71**, 1075–1080. (doi:10.1016/j.anbehav.2005.07.023)
20. Kunc HP, Amrhein V, Naguib M. 2005 Seasonal variation in dawn song characteristics in the common nightingale. *Anim. Behav*. **70**, 1265–1271. (doi:10.1016/j.anbehav.2005.02.010)
21. Foote JR, Fitzsimmons LP, Mennill DJ, Ratcliffe LM. 2008 Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behav. Ecol*. **19**, 1192–1199. (doi:10.1093/beheco/arn087)
22. Burt JM, Vehrencamp SL. 2005 Dawn chorus as an interactive communication network. In *Animal communication networks* (ed. PK McGregor), pp. 320–343. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511610363.019)
23. Cuthill IC, Macdonald WA. 1990 Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. *Behav. Ecol. Sociobiol.* **26**, 209–216. (doi:10.1007/BF00172088)
24. Thomas RJ. 2002 The costs of singing in nightingales. *Anim. Behav*. **63**, 959–966. (doi:10.1006/anbe.2001.1969)
25. Stowell D, Sueur J. 2020 Ecoacoustics: acoustic sensing for biodiversity monitoring at scale. *Remote Sens. Ecol. Conserv*. **6**, 217–219. (doi:10.1002/rse2.174)
26. Sugai LSM, Silva TSF, Ribeiro JW Jr, Llusia D. 2019 Terrestrial passive acoustic monitoring: review and perspectives. *BioScience* **69**, 15–25. (doi:10.1093/biosci/biy147)
27. Sueur J, Farina A. 2015 Ecoacoustics: the ecological investigation and interpretation of environmental sound. *Biosemiotics* **8**, 493–502. (doi:10.1007/s12304-015-9248-x)
28. SoIB. State of India's birds. 2023 Range, trends, and conservation status. *SoIB Partnership*. ()
29. Pascal JP, Ramesh BR, de Franceschi D. 2004 Wet evergreen forest types of the southern Western Ghats, India. *India. Tropic. Ecol.* **45**, 281–292.
30. Mudappa D, Raman T. 2007 Rainforest restoration and wildlife conservation on private lands in the Western Ghats. In *Making conservation work* (eds G Shahabuddin, M Rangarajan), pp. 210–240. Ranikhet, India: Permanent Black.

31. Ramesh V, Hariharan P, Akshay VA, Choksi P, Khanwilkar S, DeFries R, Robin VV. 2023 Using passive acoustic monitoring to examine the impacts of ecological restoration on faunal biodiversity in the Western Ghats. *Biol. Conserv*. **282**, 110071. (doi:10.1016/j.biocon.2023.110071)
32. Hill AP, Davies A, Prince P, Snaddon JL, Doncaster CP, Rogers A. 2019 Leveraging conservation action with open-source hardware. *Conserv. Lett*. **12**, e12661. (doi:10.1111/conl.12661)
33. The Cornell Lab of Ornithology. 2014 Raven Pro: interactive sound analysis software (v. 1.5). Ithaca, NY: K. Lisa Yang Center for Conservation Bioacoustics. See https://www.ravensoundsoftware.com/software/raven-pro/.
34. Thieurmel B, Elmarhraoui A. 2017 suncalc: compute sun position, sunlight phases, moon position and lunar phase. *CRAN: Contributed Packages*. Vienna, Austria: R Foundation for Statistical Computing. ()
35. R Core Team. 2022 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
36. Tobias JA *et al*. 2022 AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett*. **25**, 581–597. (doi:10.1111/ele.13898)
37. Tobias JA, Sheard C, Seddon N, Meade A, Cotton AJ, Nakagawa S. 2016 Territoriality, social bonds, and the evolution of communal signaling in birds. *Front. Ecol. Evol* **4**, fevo.2016.00074. (doi:10.3389/fevo.2016.00074)
38. Pinheiro J, Bates D, R Core Team. 2024 nlme: linear and nonlinear mixed effects models. v.3.1.165. ()
39. Paradis E. 2012 *Analysis of phylogenetics and evolution with R*. New York, NY: Springer. (doi:10.1007/978-1-4614-1743-9)
40. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
41. Schliep KP. 2011 phangorn: phylogenetic analysis in R. *Bioinformatics* **27**, 592–593. (doi:10.1093/bioinformatics/btq706)
42. Freckleton RP, Harvey PH, Pagel M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat*. **160**, 712–726. (doi:10.1086/343873)
43. Amrhein V, Kunc HP, Naguib M. 2004 Non-territorial nightingales prospect territories during the dawn chorus. *Proc. R. Soc. Lond. B* **271**, S167–S169. (doi:10.1098/rsbl.2003.0133)
44. Liu WC, Dawn KDE, Sparrows D. Dawn and daytime singing behavior of chipping sparrows (*Spizella passerina*). *Auk* **124**, 44–52. (doi:10.1093/auk/124.1.44)
45. Sridhar H, Beauchamp G, Shanker K. 2009 Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav*. **78**, 337–347. (doi:10.1016/j.anbehav.2009.05.008)
46. Hariharan P, Bangal P, Sridhar H, Shanker K. 2022 Habitat use by mixed-species bird flocks in tropical forests of the Western Ghats, India. *J. Trop. Ecol*. **38**, 393–400. (doi:10.1017/s026646742200030x)
47. Raman T. 2001 Community ecology and conservation of tropical rainforest birds in the southern Western Ghats, India. PhD Thesis, Bangalore, India. Indian Institute of Science.
48. Chen WM, Lee YF, Tsai CF, Yao CT, Chen YH, Li SH, Kuo YM. 2015 Dawn chorus variation in East-Asian tropical montane forest birds and its ecological and morphological correlates. *Contrib. Zool*. **84**, 255–265. (doi:10.1163/18759866-08403005)
49. Ey E, Fischer J. 2009 The 'acoustic adaptation hypothesis'—a review of the evidence from birds, anurans and mammals. *Bioacoustics* **19**, 21–48. (doi:10.1080/09524622.2009.9753613)
50. Morton ES. 1975 Ecological sources of selection on avian sounds. *Am. Nat*. **109**, 17–34. (doi:10.1086/282971)
51. Rhinehart TA, Chronister LM, Devlin T, Kitzes J. 2020 Acoustic localization of terrestrial wildlife: current practices and future opportunities. *Ecol. Evol*. **10**, 6794–6818. (doi:10.1002/ece3.6216)
52. Naguib M. 2005 Singing interactions in songbirds: implications for social relations and territorial settlement. In *Animal communication networks* (ed. PK McGregor), pp. 300–319, 1st edn. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511610363.018)
53. Fisher DN, Kilgour RJ, Siracusa ER, Foote JR, Hobson EA, Montiglio P, Saltz JB, Wey TW, Wice EW. 2021 Anticipated effects of abiotic environmental change on intraspecific social interactions. *Biol. Rev*. **96**, 2661–2693. (doi:10.1111/brv.12772)
54. Pérez-Granados C, Schuchmann K. 2021 Passive acoustic monitoring of the diel and annual vocal behavior of the black and gold howler monkey. *Am. J. Primatol*. **83**, e23241. (doi:10.1002/ajp.23241)
55. Ramesh V. 2025 Vjjan91/Diurnal-Acoustics: Zenodo Release v1.0 for Publication (v1.0). Zenodo. (doi:10.5281/zenodo.14926097)
56. Ramesh V, Sundar P, Srivathsa M, Symes L. 2025 Supplementary material from: Why is the early bird early? An evaluation of hypotheses for avian dawn-biased vocal activity. Figshare. (doi:10.6084/m9.figshare.c.7837884)